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Terrestrial Fungi

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I. Introduction

A very large number of fungi have been described and estimates of the total are open to discussion (see Ainsworth, 1971). The number of species may be at least 100,000 or perhaps as many as 250,000. Of these, a minority in normal circumstances appear to require the presence of a living host. These include various mycorrhizal fungi and the obligate biotrophs, which parasitize their hosts without killing them. The remaining fungi are either

unspecialized necrotrophs which are facultative parasites, able to live on the dead remains of the host, or saprophytes. These are the fungi which play a large part in the decomposition of plant litter. In this context, litter is taken to include not only leaves, branches, roots and woody remains, but also man-made litter such as paper and its products, textiles and plastics made from cellulosic materials and worked wood. There is a convergence of naturally occurring and anthropocentric litter, as ultimately the materials are degraded in a similar manner regardless of their immediate origin. The exception to this generalization is found in plastics which have been derived from coal or oil and are thus partly or wholly derived from plant materials, where the synthetic polymers may be highly resistant to microbial attack. Such resistance may be caused by the hydrophobic nature of the polymers together with a high level of intermolecular forces. Ways of avoiding the breakdown of plastics include the incorporation of specific antioxidants. However, if a short-lived polymer is required, then such antioxidants should be avoided. Hydroperoxides in the plastics act as powerful photoactivators for autoxidation in the presence of ultraviolet light, and have the practical effect of reducing chain length so that micro-organisms can attack and degrade these small molecules (Eggins *et al.*, 1971).

On litter derived directly or indirectly from plants fungi are able to grow whenever they possess the necessary enzyme systems and when the environmental conditions allow. Within these conditions must be included the biological component, as the fungi must be good competitive saprophytes (Garrett, 1951) to be able to exploit the substrate fully. The ability of fungi to grow on a substrate will determine their role in the decomposition of that material. The methods used to study the presence or activity of fungi in a particular habitat, however, will influence the results: all isolation techniques are selective to a greater or a lesser degree, while observational techniques which enable a fungus to be seen on the substrate do not always allow the identification of that fungus.

In a historical sense, although fungi have been described on aerial parts of plants for 100 years or more, the main emphasis for many years was on fungi in the soil, in the rhizosphere and in mycorrhizal associations. Only in relatively recent years has attention been directed at leaf-litter fungi and still more recently at phylloplane organisms. These studies have shown that leaves become colonized as soon as they unfold, or even before the bud bursts. Decomposition is thus initiated before the leaf is even mature. Harley (1971) has recently discussed the role of fungi in ecosystems showing the part which they play in decomposition processes, and how they in turn can become sources of nutrients for other organisms. Some aspects of fungal activities are considered in this chapter.

II. Ecology

In studying the ecology of fungi on plant litter, the early emphasis was on soil fungi, where an awareness of substrate relationships gradually evolved. The surface covering of plant litter, however, was relatively neglected: Chesters (1960) complained that litter lying on the soil had scarcely been looked at, indeed that it was "thrust aside in an effort to get at the 'soil'."

A. Fungi on Plants

In studying the ecology of fungi associated with plant material, several processes must be considered. The plant arises from a seed which had a mycoflora. The seed coat fungi may include some potential pathogens: there will certainly be a number of fungal saprophytes (see Malone and Muskett, 1964). The role of these saprophytes in the colonization of the germinating seedling is probably not great under normal agricultural conditions. Their influence on the colonization of roots was studied by Peterson (1959), who found that fungi associated with seeds of barley, flax and wheat played little part in the colonization of roots in the soil, Similarly, Catska *et al.* (1960) reported that soil fungi were more apparent on the roots of wheat seedlings than were seed-borne fungi. Seeds which have been surface sterilized have also been used for studying the fungal colonization of seedling roots: Parkinson *et al.* (1963) found that a mixed fungal population was at first present, but that this rapidly became stabilized into a typical root-surface mycoflora. A similar picture was presented by Stenton (1958), who isolated over 40 different fungi from pea roots; of these the genera *Cylindrocarpon*, *Pythium*, *Fusarium*, *Gliocladium* and *Mortierella* were abundant. He reported that fungi spread rapidly along roots until they reached an already occupied area. However, Taylor and Parkinson (1961) suggested that lateral colonization of roots by fungi in the soil is more important than growth of fungi along the roots.

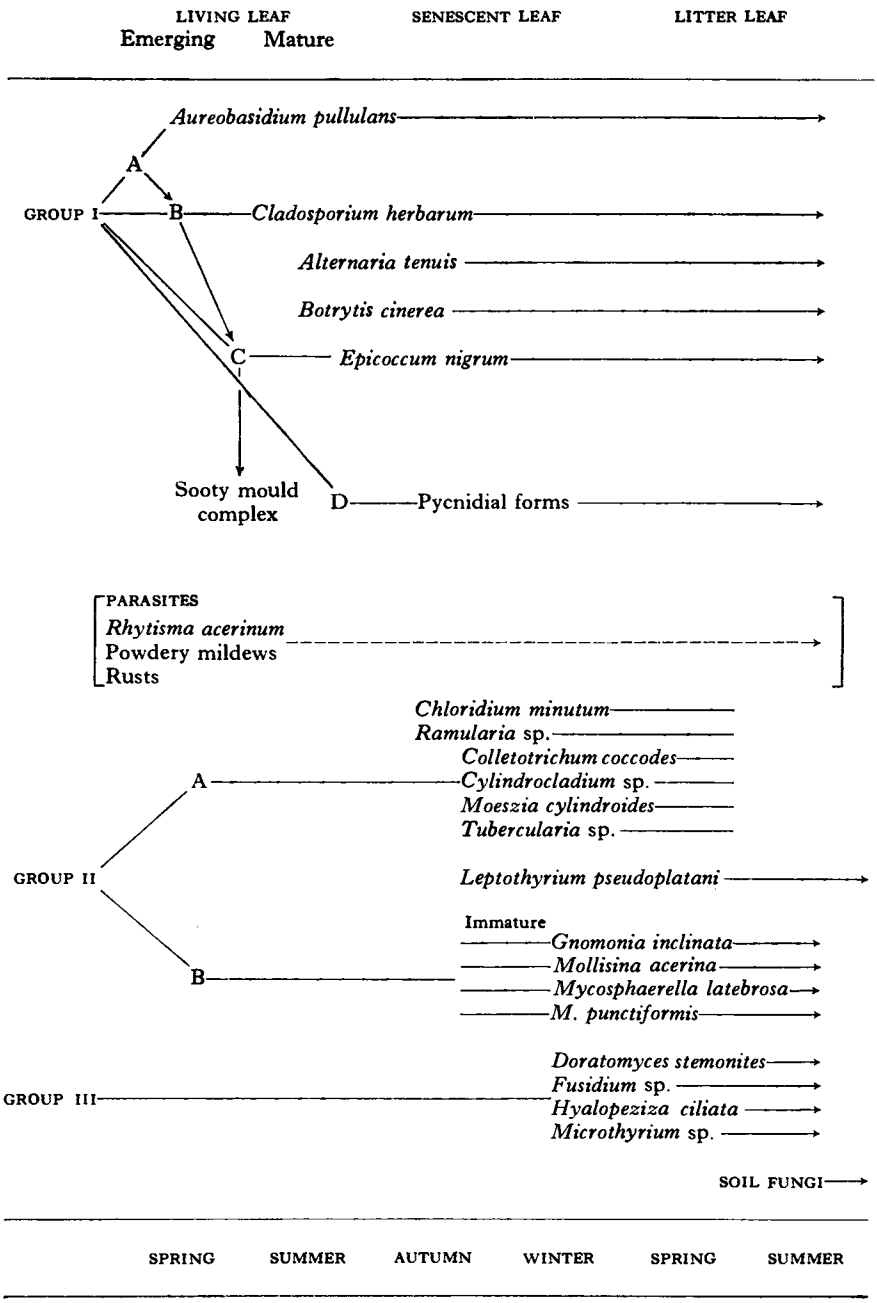
In soils with an impoverished mycoflora, and where conditions adverse to fungal growth are prevalent, the seed coat fungi may play a more important part in root colonization. Thus Pugh and Dickinson (1965) showed that roots of seedlings of *Halimione portulacoides* (L.) Aell. growing in salt marsh muds were at first dominated by fungi present on the seeds and in the mud, and they suggested that there may be a joint source of inoculum, while Pugh (1960) found that mature roots of *Salicornia stricta* agg. growing in the same salt marsh, were colonized by *Dendryphiella salina* (Sutherland) Pugh & Nicot and a sterile white mycelium. These two fungi were also isolated from the seeds, but not from the muds in which the plants were growing.

The influence of the seed mycoflora on the aerial parts of plants has been relatively little studied. However, Pugh and Buckley (1971*a*) showed that *Aureobasidium pullulans* (de Bary) Arnaud could be isolated from the surface-sterilized seeds of sycamore (*Acer pseudoplatanus* L.), from the testa after removal of the pericarp, and from the embryo. It was also found on the hypocotyl and on the young roots of the seedlings. Buckley and Pugh (1971) showed that *A. pullulans*, *Cladosporium herbarum* Link and *Epicoccum purpurascens* Ehrenb. ex Schlecht. can produce auxins in the laboratory and Pugh (1973) indicated that the presence of the seed coat mycoflora may aid the germination of sycamore seeds.

Aureobasidium pullulans can also be isolated from the first opening of the buds, and is thus present on the leaves as the first of the primary colonizers. It has the ability to decompose pectin (Smit and Weiringa, 1953). It is joined by both yeasts and filamentous fungi which are able to grow in the hostile environment of the leaf surface: the majority are coloured or pigmented, and this is known to afford protection against harmful radiations. Thus *Rhodotorula* and *Sporobolomyces* are common yeasts. *S. roseus* Kluyver & van Niel has been shown by McBride (1972) to affect the leafy surface waxes. Amongst the filamentous fungi, *Cladosporium* spp. (mainl-*C. cladosporioides* (Fresen.) de Vries and *C. herbarum*) become abundant on the mature leaf, at a time more or less corresponding to their peak occurrence in the atmosphere. Many workers have found that *Cladosporium* spp. do not grow on leaves until they become senescent (e.g. Bainbridge and Dickinson, 1972). However Pugh and Buckley (1971*b*) reported the growth and sporulation of *Cladosporium* on green leaves of sycamore from July onwards. Other fungal colonists which arrive on the living leaves later in the year include *Alternaria alternata* (Fr.) Keissl., *Botrytis cinerea* Pers. ex Fr., *Epicoccum purpurascens*, as well as pycnidial and perithecial forms which remain as sterile hyphae on the living leaves and develop their fructifications after leaf-fall. Thus Dickinson (1965), working with phylloplane fungi on *Halimione portulacoides*, included *Ascochytula obionis* (Jaap) Died. in this third category.

The colonization of sycamore leaves from the bursting of the buds, throughout maturity and senescence, until they are decomposing on the ground, is summarized in Table I. After the arrival of *Cladosporium* and *Epicoccum*, *A. pullulans* appears to be present only as chlamydospores and microsclerotia on the leaf surface; after the leaf has been lying on the ground over winter, *Cladosporium* also is present in the form of microsclerotia. Pugh and Buckley (1971*b*) suggested that isolations of these fungi from old leaf litter and from the soil may indicate the survival of such resting stages rather than any activity on the part of the fungi. Last and Deighton (1965) reviewed in detail the occurrence of fungi on leaf surfaces,

TABLE I. Stages in the succession of fungi on leaves of *Acer pseudoplatanus* (from Buckley, 1971)



and Hudson (1968) and Bell (Chapter 2) have given comprehensive accounts of fungi on aerial part of plants.

A wide range of methods has been used in the study of fungi on aerial parts of plants. Studies on fungal successions on leaves and leaf litter illustrate the necessary adoption of several complementary methods. As Dickinson (1971) said, "Progress in phylloplane studies will only be achieved by selecting suitable combinations of these cultural methods and by allying such work with direct or indirect microscopic examination of the leaf surface and with physiological and biochemical investigations of pure cultures of leaf saprophytes." Lindsey (1973) has analysed the techniques used in studies of fungal succession since 1955. In the years 1955–1960, five techniques were used: spore fall, damp chambers with examination after two or after seven or more days' agar culture of leaf portions, and surface sterilization before culture. Between 1961 and 1966 three more techniques were used: direct observation of leaves, and of cellulose acetate films of the easily removable particles on leaf surfaces, together with the cultivation of the organisms present in water used to wash leaves. During the years 1967–1972 an additional four methods have been used in the studies of fungal successions: maceration followed by cultivation of the fungi in the particles; the use of pectinase to separate the cells so that individual leaf parts (the cuticle or the vascular system, for example), can be incubated to see where fungi are present in a leaf; clearing of the leaf before direct examination in transmitted light; and the scanning electron microscope, which has illustrated the presence of spores and hyphae on the surfaces of living leaves and leaf litter (Fig. 1). Many of these techniques had been used in other studies, for example in plant pathology, but their use in successional studies is relatively recent. Lindsey was also able to show that in his three-year groups, the number of techniques used, and the mean number of techniques per study rose from 5 and 1·6 respectively in 1955–1960, to 8 and 2·4 in 1961–1966 and to 12 and 3·5 in 1967–1972. The parallel use of isolation techniques with observation of surfaces of freshly collected leaves is most important in arriving at an understanding of fungal activity on the leaves.

B. Fungi in the Soil

The soil can be regarded as a reservoir into which fall spores and other propagules of fungi whose active life is above the soil, and plant material already colonized by fungi. These join the fungi which normally inhabit the soil, and they may grow and successfully compete with the soil fungi, or more frequently they may not be able to compete and may gradually disappear from the soil. During the last 60 years a great array of techniques

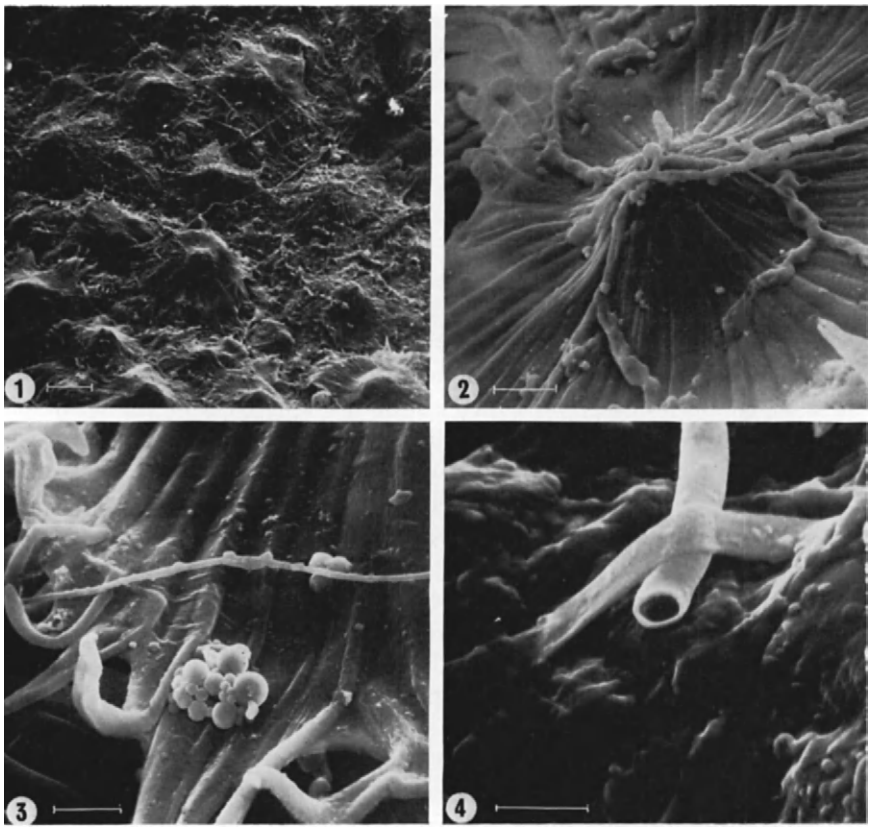


Fig. 1. Fungi on the surface of fresh litter leaves of *Hippophae rhamnoides* collected in November.

1. Trichomes with hyphae growing over them.
2. Hyphae and scattered spores on a trichome.
3. Hyphae and a young sporodochium of *Epicoccum purpurascens* on a trichome.
4. Severed hypha on a trichome, possibly bitten by a member of the microfauna.

Scale line on A = 100 μm; on B, C and D = 10 μm.

has been evolved to evaluate the soil mycoflora qualitatively and quantitatively (see Warcup, 1960, 1967; Johnson and Curl, 1972; Parkinson *et al.*, 1971). In 1916 Waksman suggested a hypothetical flora of the soil which would "consist of several species of Aspergilli, more than those types (not always in numbers) of Mucors and Penicillia, together with the green Trichodermae; besides these, one would expect to find a *Zygorhynchus*, one or two species of Cladosporia, *Alternaria*, *Rhizopus*, Fusaria, Verticillia, Cephalosporia, associated perhaps with an *Acrostalagmus*, a *Scopulariopsis*, a *Botrytis*, some sterile mycelium and one or two yeasts . . .". He

regarded the aspergilli as being more prevalent in tropical soils and the penicillia as more abundant in temperate regions. The cosmopolitan nature of these genera in the soil was borne out 56 years later by Domsch and Gams (1972), who carried out a massive series of isolations in two areas of northern Germany. They obtained 23,500 isolates, covering 209 species. Their survey of the literature on these species showed "more and more soil fungi to be ubiquitous, with a virtually worldwide distribution."

During the course of the floristic studies of the soil mycoflora the question was raised as to what the fungi were doing in the soil: were they merely there as propagules, or were they actively growing? In attempts to answer this question a number of techniques were used to distinguish between these states. Each in turn presented a situation equivalent to the "Principle of Uncertainty", i.e. would the result have been the same if the technique had not been applied, or did the application of the technique so alter conditions that fungal growth became possible? Thus those techniques which involve the insertion of a glass slide or a nutrient substrate into the soil provide new uncolonized space, as well as altering the nutritional status, and the physical characteristics of the soil such as the water regime. The nutrients are also attractive to members of the soil fauna, which carry spores on and in their bodies and thus are a source of inoculum. Techniques which involve taking soil samples to the laboratory normally involve incubating soil crumbs on nutrient media, where spores can germinate. The use of embedding methods (e.g. Nicholas *et al.*, 1965) showed the presence of hyphae in the soil, but could not distinguish between living and dead mycelium and normally cannot be used to identify the fungi. The hyphal isolation method (Warcup, 1957) can be used to indicate species which at some point in time have grown in that soil, but as Warcup pointed out "the presence of viable hyphae need not be synonymous with active growth in soil" immediately prior to isolation.He also emphasized that the method of investigation will greatly influence the picture obtained of the types of activity of the fungi in the soil. Further evidence for such influence was given by Pugh (1969) who showed that the use of cellulose agar (Eggins and Pugh, 1962) eliminated members of the Phycomycetes from the fungi isolated from the soils studied, and also more than doubled the isolation rate of the Dematiaceae. Other selective techniques have been devised specificially to isolate particular ecological or nutritional groups of fungi. There are comprehensive lists of methods used in soil mycology in Johnson and Curl (1972), and critical evaluations are given by Warcup (1960, 1967), and Parkinson *et al.* (1971).

The present situation is that the generally used techniques cannot distinguish between dormant and actively growing fungi in an unaltered

soil. However, in certain situations, such as the growth of fungi along an elongating root, or in the use of labelled isotopes incorporated into a medium to trace the spread of hyphae able to translocate those isotopes, fungal growth can be measured without altering the micro-environment. Other methods, such as respirometry or analyses of enzyme production, can indicate total activity within a complete soil sample or the activity of individual organisms in a previously sterilized soil.

Harley and Waid (1955) summed up the difficulty of use of techniques by emphasizing that the methods must be able to "distinguish between organisms which are vegetatively active and playing a part in the soil processes and those which exist as dormant or inactive forms as spores and other propagules." Another point of view was expressed by Pugh (1969) who said that while the phase of active growth is important, spores and other propagules are formed in the soil as a result of previous activity and are normally a concomitant of, and evidence for that activity. This view had arisen from the transient nature of the substrates described as "finite and exhaustible" by Garrett (1951), which are colonized by a succession of fungi able to grow on the available part of the substrate and which then sporulate and die down; the inability of techniques to distinguish active growth, and from the earlier use of the term "fungal potential", which was defined as "active mycelium plus propagules which are the result of previous activity, held dormant by such factors as mycostasis" (Pugh, 1963). Within the soil the amount of organic matter normally diminishes with increasing depth, as does the frequency of isolation of fungi. However this is not merely a reflection of the relationship between organic content and fungi, as a similar decrease in fungal isolations also occurs in peat soils. The growth of fungi on the organic particles led Chesters (1948) to devise his soil-washing technique, which enabled the organic fraction to be separated from the mineral particles, while the propagules were generally removed with the washing water. This technique was elaborated by Williams *et al.* (1965) and has since been regularly used to study the fungi on organic particles in a variety of soils. This emphasis on the substrate has also resulted in the development of various media and methods for the selective isolation of nutritional groups of fungi. Of these the cellulose-decomposers have received much attention if only because cellulose forms such a large proportion of plant material. Amongst the methods are those of Tribe (1957) who buried strips of "Cellophane" attached to cover slips, Webley and Duff (1962), who used kaolinite pellets in which individual substances, including cellulose, had been incorporated, and Eggins and Pugh (1962) who incorporated ball-milled cellulose powder into an agar medium so that cellulolytic activity could be detected by a clearing of the previously opaque medium.

The picture of the soil that has emerged is of a system of organic microhabitats dispersed through an essentially mineral matrix. Each microhabitat has its mycoflora which may be active, quiescent or dormant. However, there is other organic matter in the form of humus which may be deposited on the mineral particles, and stem structures (rhizomes, bulbs, corms) present at various depths, and as a major influence there are roots of plants growing down through the soil profile, which may have mycorrhizas growing into the litter layers. Each of these living structures can profoundly affect the microflora in the soil. Their exudates include amino acids and sugars, while sloughed-off materials include root cap cells, root hairs and external tissues after secondary thickening (see Dickinson, Chapter 20). Micro-organisms grow and flourish on these additional substrates, creating the rhizosphere effect. Associations between soil micro-organisms and roots have been considered by Parkinson (1967), and the decomposition of roots is reviewed by Waid (this volume Chapter 6).

III. Biology

A. The Thallus

The basic vegetative form of the fungi is a thallus which may be a structurally simple cell, or a system of branched hyphae which may fuse or anastomase to form complex sporophores. The form of the thallus can conveniently be divided into three groups: (i) the unicellular, uninucleate thallus as in the chytrids and the yeasts; (ii) the unicellular, multinucleate thallus (coenocyte) found in filamentous, phycomycetous fungi such as *Saprolegnia* and *Mucor*; (iii) the multicellular thallus. This may have a single haploid nucleus in each cell; or a single diploid nucleus in specialized reproductive cells such as the ascus initial and the young basidium; it may have two compatible but heterocaryotic nuclei, as in the dicaryotic mycelia of Basidiomycetes; or there may be several nuclei in each cell. These may be genetically different (heterocaryotic) or similar (homocaryotic). Somatic variations can arise in heterocaryotic mycelia when different nuclear combinations occur in branches or as a result of anastomoses between hyphae. They can also arise during sporogenesis. Such changes can result in great differences in the physiology and metabolism of morphologically similar isolates of a given fungus. Morphological change can also occur and can be seen as a "sector" in a culture growing on agar media.

1. Hyphal Morphology

In filamentous fungi the basic structural unit is the hypha. Hyphae arise as tubular outgrowths from the germinating spore, and grow by extension

of the hyphal apex. The wall of the hyphae is composed mainly of polysaccharides, which account for 80–90% of the wall. In addition there are proteins, lipids and polyphosphates. Peberdy (1972) has reviewed fungal wall structure, an understanding of which is necessary in his work on fungal protoplasts. He has indicated that there are at least 11 monosaccharides present in the walls. Of these, D-glucose is present as 1-3β and 1-6β linkages in glucans, 1-6β polymers of *N*-acetylglucosamine in chitin and D-mannose with α and β links mainly 1-3 and 1-6 in mannans. Most fungi have chitin, which accounts for up to 60% of the wall dry weight. Cellulose is found only in the walls of members of the Oomycetes.

As the hyphae grow they produce septate or non-septate filaments which normally branch in a racemose manner, and which collectively form the mycelium. In some fungi the hyphae become aggregated into cord-like mycelial strands, which are formed around a central hypha by branches which interweave and anastomose, or rhizomorphs, in which closely associated parallel unbranched hyphae grow as a single unit from an apical meristematic region. Garrett (1970) has calculated that there will be several thousand hyphae in a rhizomorph 1 mm in diameter. He and his co-workers have studied the morphogenesis and behaviour of strands and rhizomorphs and they found that the leading hyphae, around which strands of *Serpula* (*Merulius*) *lacrymans* (Pers.) ex Gray form exude nutrients which attract the investing hyphae, and this close association leads on to the development of anastomoses between compatible hyphae.

Townsend (1954) studied the development of rhizomorphs of 16 species of Basidiomycetes and arranged them into a series showing increasing differentiation. Pugh (1969) interpolated this scheme into an earlier one of Garrett (1944), to form a continuum from individual hyphae of *Rhizoctonia solani* Kuhn to complex, zoned rhizomorphs of *Armillaria mellea* (Fr.) Quel. (Table II), via hyphal strands and rhizomorphs which showed increasing degrees of differentiation. Garrett (1970) has pointed out that the production of rhizomorph initials increases with added glucose concentration at least to the level of 2% whereas strand formation is delayed by the presence of nutrients above a low concentration.

The biological advantages of strand and rhizomorph production are probably associated with translocation of nutrients from a food base, with increased competitiveness in saprophytes and virulence in parasites, as a greater enzyme concentration or penetration ability can be brought to bear on the substrate, and certainly with an increase in the rate of growth: rhizomorphs of *A. mellea* were reported by Garrett (1970) to grow 5–13 times faster than unorganized hyphae. A further advantage is conferred on these rhizomorphs, the rind of which becomes pigmented with melanin. This does not occur when the rhizomorph is bathed in a film of water (i.e.

when the oxygen tension is low). When rhizomorphs grow into dry soil, the melanin is able to form a mycostatic layer over the apex, and growth ceases.

2. Asexual Dispersal Spores

In the great majority of fungi the living mycelium grows over or through its substrate, exuding enzymes and absorbing soluble nutrients. Under these conditions asexual spores quickly form and are normally able to be dispersed. The method of formation of the spores is used as a criterion in

TABLE II. Runner hyphae, mycelial strands and rhizomorphs (from Garrett, 1944, and Townsend, 1954)

I. Hyphae and mycelial strands	
1. *Rhizoctonia solani*	individual hyphae
2. *Ophiobolus graminis*	individual hyphae and occasional strands
3. *Helicobasidium purpureum*	undifferentiated strands
4. *Phymatotrichum omnivorum*	strands with distinct differentiation
II. Rhizomorphs	
5. *Fomes lignosus*	undifferentiated rhizomorphs
6. *Collybia platyphylla*	different arrangement of similar hyphae
7. *Psalliota campestris*	hyphae of different sizes forming zones
8. *Armillaria mellea*	hyphae differ in size and structure forming distinct zones

the classification of fungi. The spores in fungi may be unicellular or multicellular, with each cell able to produce a germ tube: such multicellular spores may be considered as groups of one-celled spores (Sussman and Halvorson, 1966). The spores may be formed within a sporangium (sporangiospores): these may be motile, with one flagellum or two, or they may be non-motile. Conidia are asexual dispersal spores which arise singly or successively on hyphae, and are thus distinct from sporangiospores which arise simultaneously and endogenously. Uredospores and aecidiospores may be regarded as specialized conidia in the Rust Fungi (Uredinales). Teleutospores (Uredinales), which are not dispersed, and brand spores (Ustilaginales) are biologically similar in that nuclear fusion occurs in them prior to basidium formation and both act as resting spores but their ontogeny is very different (see Moore, 1972).

3. Dispersal

Spores become disseminated by many agencies. Amongst them are air currents; water, including raindrops; animals, including man, insects

and earthworms; and soil. Dispersal has been fully discussed by Ingold (1971).

Air movements are by far the most important, both for localized dispersal, for example in convection currents in a room, and also for long distance transport. Within the atmosphere fungal spores form the largest proportion of the air spora, and they have to withstand many adverse conditions which can affect their viability. Gregory (1973) has discussed the survival of spores in the atmosphere and said that exposure to radiations, particularly near the ultraviolet wavelengths, was a serious hazard: in the upper atmosphere when spores are not sheltered by clouds they receive relatively high dose rates. Many fungi which sporulate on the aerial parts of plants, including pathogens, have spores which are protected from the harmful effects of radiations by pigmented walls or by the presence of carotenoids. These would fit into Gregory's group of "hardy microbes"; others which do not appear to have any such protection were regarded as "tender pathogens", a term which could be expanded to include saprophytes such as *Aureobasidium pullulans* and the hyaline yeasts.

Other adverse factors affecting spores include the risk of desiccation, which is greatest in daytime and in the lower air layers. At higher altitudes and at the lower night temperatures evaporation is reduced. Temperature fluctuations were also considered, but were thought to be not great, as the minute size of the spores would allow them to equilibriate quickly with the surrounding air. The combination of low temperatures and desiccation may help combat radiation damage to spores. At the same time "lowering the water content of organisms mitigates the lethal effects of temperature extremes" (Sussman and Halvorson, 1966), although they point out that dehydration can also be injurious or even lethal.

Gregory (1973) has discussed at length the ways in which spores are removed from the atmosphere. Three common phenomena are sedimentation under the influence of gravity in still air; impaction of spores being moved in air currents which go around an object while the spore is carried on to the object by its momentum; and boundary layer exchange when eddies of spore-laden air get into the relatively still air near the ground, or when they are injected into the spore-free laminar air layer immediately around an object. The spores then settle out of the air by sedimentation. In addition to these methods of deposition, the effect of rain on the air spora is very great and has been described as "rain scrubbing". This was regarded as "an ideal method of deposition for air-dispersed soil fungi" (Hirst, 1959), although the biological significance of rain deposition of spores of leaf pathogens was not clear, as they could be washed off the leaf surface. They could, however, be retransported to the leaves in splash droplets.

B. Resting Propagules

As a fungus grows on its substrate it produces spores which are usually asexual sporangiospores or conidia and which disperse the fungus spatially. The fungus may also grow out from its substrate by means of hyphae, or mycelial strands or rhizomorphs. However, it may also, or alternatively, produce a resting state, which extends the duration of the fungus in time (Garrett, 1956). The resting form of the fungus may arise as a result of sexual reproduction or it may represent a changed state of the vegetative mycelium.

Spores associated with sexual reproduction vary greatly in form, size and method of production. In the Saprolegniales (water moulds) the oospores are formed within oogonia; the zygospore of the Mucorales is produced from the fusion of two multinucleate gametangia; ascospores are formed endogenously after nuclear fusion and meiosis in the ascus initial; basidiospores arise exogenously on a basidium in which the dicaryotic nuclei have fused and divided meiotically.

Other types of resting spore associated with sexual reproduction are the teleutospore and the brand spore. Teleutospores are formed on the host towards the end of the growing season by members of the Uredinales, and act as overwintering spores; brand spores (Ustilaginales) form on or in the host and may be dispersed. Both are dicaryotic and germinate to produce a basidium from which basidiospores arise.

Within an individual hypha the apex contains dense, nonvacuolate cytoplasm. This soon becomes vacuolate, and as the hypha ages the cytoplasm dies leaving a cylindrical shell of wall material. Parts of the living mycelium may form chlamydospores, which represent cells in which the cytoplasm has become condensed and the wall thickened. These are generally intercalary, but can be terminal and are found in such common genera as *Fusarium*, *Mucor* and *Trichoderma*. They can be seen as remnants of once-living hyphae, although they may be undetected inside organic particles in the soil.

Sclerotia are more complex but biologically similar structures. They may act simply as vegetative resting organs and give rise to hyphae in due course. Alternatively they may germinate to produce asexual spores, as in *Botrytis* spp., or they may develop to produce stromata in which organs of sexual reproduction are formed, as in *Claviceps purpurea* (Fr.) Tul., or sporophores as in *Sclerotinia sclerotiorum* (Lib.) de Bary.

Sclerotia consist of a mass of living hyphae, and broadly, can be grouped into those with no definite pattern of organization of the hyphae, so that a loose structure is formed in which there are no well defined zones, and those with a surface covering, or rind. The internal tissues may be further differentiated into a cortex and medulla. Townsend and Willetts

(1954) gave an account of earlier studies on sclerotial structure and described the development of sclerotia in a range of fungi, distinguishing three methods of formation. Their "loose" type arose from an aggregation of adjacent hyphae and their side branches of short, barrel-shaped cells which have dense contents and no vacuoles. These are found in *Rhizoctonia solani*. Their other two types both have a rind at maturity. In their "strand" type, found in *Sclerotinia gladioli* Drayton, numerous lateral branches develop from one or more axis hyphae, and may lie parallel with them or at right angles to them. They may branch again before fusing and coalescing with each other. At maturity there is a medulla of large thin-walled cells enclosed within the rind. In *Phymatotrichum omnivorum* (Shear) Duggar both cortex and medulla are present. Their "terminal" type was described from *Botrytis allii* Munn., and they found a somewhat similar development in *B. cinerea* and at least initially in *Sclerotium cepivorum* Berk. The hyphal apex branches repeatedly and dichotomously, with the formation of cross-walls, until the hyphal mass coalesces to form the sclerotium, in which there are rind, a narrow cortex of pseudoparenchyma and a large central medulla of loosely arranged filaments. More recently, Coley-Smith and Cooke (1971) have reviewed the structure, survival and germination of sclerotia, which, as they pointed out, have been most studied in plant pathogenic fungi.

C. Dormancy

While many spores are able to germinate as soon as they become detached from their parent hyphae, others remain in a dormant state until they are able to germinate. Two types of dormancy, constitutive and exogenous, have been recognized and these apply to both sexually produced and vegetative resting stages. These have been defined by Sussman and Halvorson (1966) as: Constitutive dormancy: a condition in which development is delayed due to an innate property of the dormant stage such as a barrier to the penetration of nutrients, a metabolic block, or the production of a self-inhibitor. Exogenous dormancy: a condition in which development is delayed because of unfavourable chemical or physical conditions of the environment".

Once a resting structure has overcome any constitutive dormancy it may then be held in a state of exogenous dormancy until there are favourable environmental conditions. Most work in this field has been carried out with plant parasites, in which survival times of several years may be encountered. In considering the role of fungi in the breakdown of plant remains, one aspect of exogenous dormancy has received considerable attention. This is the phenomenon of mycostasis.

D. Mycostasis

The soil can be regarded as a habitat in which spores form as the result of the activity of the parent mycelia, and into which spores fall or are washed after being dispersed. Sussman and Halvorson (1966) mentioned a number of observations of the presence of substances which inhibit spore germination in the soil. Dobbs and Hinson (1953) described the phenomenon of spores remaining ungerminated in the soil. They showed that this was a widespread occurrence which affected the spores of several different species. Later workers have shown that mycostasis (also referred to as fungistasis) affects fungal spores on a worldwide basis: for example Jackson (1958) in Nigeria, Lingappa and Lockwood (1961) in Michigan and Knaphus (1964) in Iowa, U.S.A., Cooke (1967) in Iceland. The possible causes of inhibition have also received attention (see Forbes, Chapter 23). It has been known that the addition of glucose will stimulate germination of the spores as will exudates from roots; but mycostasis is more than an absence of nutrients: there is an inhibitory factor present which can be overcome by the addition of a suitable substrate. Inhibition can be overcome by heating the soil, and there is some evidence that an inhibitor can be extracted from soil, although results have been erratic. Among the possible inhibitors must be considered antibiotic metabolites, which could be staling products. Balis and Kouyeas (1968) have suggested that a volatile factor is involved, and that it could be an unsaturated hydrocarbon or its derivative. Certainly volatile inhibitors can be produced which affect radial extension growth of fungi. Dick and Hutchinson (1966) showed that volatile metabolites of two yeasts and of *Fomes annosus* (Fr.) Cooke produced significant inhibition of growth of various test fungi.

The leaching of nutrients from the spore could encourage the growth of competing organisms. Lingappa and Lockwood (1964) reported a 7-fold increase in both bacterial numbers and soil respiration when living fungal spores, or water used to wash them, were added to the soil. This implies that the exudates from the spores could act as a trigger for the germination of those spores if the exudates are not leached away or utilized by competing micro-organisms.

The type of mycostasis which may be caused by or associated with the presence of soil micro-organisms was referred to as "microbial mycostasis" by Dobbs and Gash (1965). This can be removed by autoclaving and by the use of sterilizing agents, and it does not return as long as the soil remains sterile. Similarly, it is generally absent from sterile or near-sterile subsoils. There is, however, a "residual mycostasis", which they found in several calcareous soils in North Wales. This was thermostable, and was not overcome by the addition of sugars. In these basic soils the

inhibition of germination may be caused by unchelated iron, or by the presence of calcium carbonate.

E. The Fate of Hyphae and Spores

Although hyphae may be locally or seasonally abundant in particular situations, they do not accumulate in the soil or in leaf litter. There is evidence that hyphae with pigmented walls are more frequently seen in soil sections than normal isolation techniques would indicate (Burges, 1958), but Pugh (1969) suggested that this discrepancy may have been caused by the type of isolation medium used.

Many members of the soil microfauna feed on hyphae and spores, and appear to have feeding preferences. Heal (1963) showed that amoebae fed on yeasts and on 2 of 16 species of fungi which he tested. The role of fungi as food for nematodes is discussed by Twinn (Chapter 13) and for micro-arthropods by Harding and Stuttard (Chapter 15). Hyphae which are not eaten by these or other animals may autolyse, or may be utilized by soil micro-organisms. Bumbieris and Lloyd (1967) showed that in a wet soil (25% moisture content) the cell wall and its contained protoplasm disappeared concurrently, with bacteria following protozoa. In a dry soil (13% moisture content) the protoplasm was lost, leaving the hyphal walls; this was associated with Actinomycetes. In intermediate soils (19% moisture content) Actinomycetes followed bacteria on the hyphae.

Lloyd and Lockwood (1966) found that hyphae were completely lysed within 4–8 days of being added to soil, and Old (1967) showed that after 10 days only 20% of hyphal fragments of *Cochliobolus sativus* (Ito & Kurib.) Dreshs. ex Dastur survived in soil, compared with 73% of conidia which were still viable. However, few conidia survived 50 days in natural soils. A detailed account of the fate of residues of Actinomycetes, algae, bacteria and fungi in the soil has been given by Webley and Jones (1971).

F. Predacious Fungi

At various stages in the decomposition of plants, the litter becomes invaded by nematodes. In leaves of *Typha latifolia* L. for example, Pugh and Mulder (1971) found that nematodes were plentiful in the final stages of decomposition. Certain fungi prey on nematodes, trapping them in specialized, sticky branches, in complex loops, or in constricting nooses. Once the eelworm is caught, its body is invaded by hyphae, which can be seen ramifying inside. It has been suggested that a toxin is produced by the fungus which paralyses or kills the nematodes (see Olthof and Estey, 1963). Typical predacious fungi are species of *Arthrobotrys*, *Dactylaria* and

Dactylella, which are members of the Hyphomycetes, and members of the Zoopagales (Zygomycotina), which shed sticky spores. In *Arthrobotrys conoides* Drechsler, the formation of the complex loops requires the presence of CO_2 as well as "nemin", a substance produced by nematodes. Studies on the succession of predacious fungi have been carried out by Cooke (1963), while Duddington (1968) gave an account of their activities.

IV. Classification

The classification of fungi which occur in terrestrial situations virtually involves the classification of all fungi except the few which are restricted to aquatic environments (see Jones, Chapter 11). No system of classification can hope to be ideal, but each can be adapted to serve a particular purpose. Thus for purposes of identification a taxonomic approach will normally be appropriate; this may make use of arbitrarily selected characters as criteria, and result in an artificial classification; or it may aim at a classification which makes use of natural relationships and phylogeny. On the other hand there may be an ecological approach, in which organisms are grouped on their patterns of occurrence; or a biological classification based on their pattern of behaviour or a physiological approach making use for example, of nutritional attributes.

A. Taxonomy

The criteria used in fungal taxonomy are essentially all morphological, and may be selected from different stages in the life cycle. Ideally all observations of the selected criteria should be carried out on the same substrate or host under the same conditions and on the fungus at a specified age. In practice this ideal is not essential except for particular genera (e.g. *Penicillium*, *Aspergillus*). Chesters (1968) has said that criteria are not all equally valuable at a given taxonomic level. He stated that morphological criteria should show considerable constancy, as well as definite degrees of difference which would allow effective separation of taxa; the variability of each criterion should be known and accurate observations should be possible for each criterion.

Traditionally the fungi have been classified into Phycomycetes, with hyphae which characteristically lack septa, except those that cut off reproductive structures or are found in older mycelia. In some of the simpler forms there may be no vegetative thallus, or only a rudimentary one. The other three sub-divisions, Ascomycetes, Basidiomycetes and Deuteromycetes (Fungi Imperfecti) all possess septate hyphae and are distinguished by their sexually produced spores, which are endogenous,

exogenous or absent respectively. The Phycomycetes have long been recognized as a heterogeneous collection of fungi (see von Arx, 1967). Recently Webster (1970) has treated the Mastigomycotina, with a motile stage in their life cycles, as of equal rank with the Zygomycotina (with non-motile spores). Ascomycotina (Ascomycetes) and Basidiomycotina (Basidiomycetes).

Within the Ascomycetes, the system of classification has seen many changes since Miller (1949) based his revision on the type of ascus and on the ontogeny of the ascocarp, drawing attention to earlier work which recognized that loculate stromata were of different origin from perithecia.

The validity of the Basidiomycetes as an entity has been questioned by Moore (1972) who has proposed the erection of a new taxon, the Ustomycota, to be of equal rank with the Ascomycota and Basidiomycota, to accommodate the ustilaginaceous fungi.

In the Deuteromycetes, separation of form-genera has been based on the work of Saccardo (1886). The relative ease with which fungi can be placed in their pigeon-holes has made this artificial system widely used. Searches for a more natural system have centred around the method of spore production, and have resulted in the adoption of many criteria which were not previously used.

All fungi are dependent, directly or indirectly, on green plants or their products. Plant-pathogenic fungi include the biotrophs, which are generally obligate parasites and which do not normally kill the host, and necrotrophs, or facultative parasites. These can cause severe damage to the plant, and can live on the dead remains of the plant. The saprophytes grow on the dead remains of plants and animals. Some of them, however, may act as weak parasites or primary colonizers of still living plant tissues in which natural resistance has been lowered, for example, when they become moribund.

1. Mastigomycotina

The lower members of this division live in water and are generally regarded as aquatic. However, there is normally sufficient water present in the soil for their growth and reproduction. Among the plant parasitic Chytridiomycetes in soil are *Olpidium brassicae* (Woron.) Dang., which is common on roots of cabbages, and which has been implicated in the spread viruses causing big-vein disease of lettuce; and *Synchytrium endobioticum* (Sch.) Percival, which causes potato wart disease. *Rhizophlyctis* and *Nowakowskiella* are widespread saprophytes in the soil. The former occurs on cellulosic substrates and has been shown able to decompose cellulose in culture. In the Blastocladiaceae, *Allomyces*, and *Blastocladiella* can be isolated from the soil by the use of suitable baits, such as rose hips and hawthorn fruits.

Members of the Oomycetes, which have a cellulosic cell wall include the Saproleginales (the water moulds), which are discussed by Jones (Chapter 11) and the Peronosporales. Here there are many plant parasites, including the members of the Peronosporaceae (downy mildews), as well as *Pythium* and *Phytophthora*. Members of these two genera can also grow saprophytically in the soil.

2. Zygomycotina

These fungi, with no motile stages in their life-histories, are typical terrestrial fungi. In the Mucorales species of *Absidia*, *Mucor*, *Mortierella* and *Zygorrhynchus* form a significant part of the soil mycoflora, and have also been regularly isolated from plant litter. Although they have been isolated from "Cellophane" and on carboxy-methyl-cellulose, they are not normally regarded as decomposers of natural cellulose. Species of *Mortierella* are often associated with decomposition of chitin, and several members of the Mucorales (e.g. *Pilobolus*, *Pilaira*) occur regularly on dung (see Lodha, Chapter 7). They are generally considered as members of the "sugar fungi" (Burges, 1939), growing as primary colonists on newly available, simple, soluble carbohydrates. Some species can also grow as "secondary sugar fungi" (see Hudson, 1968) when they utilize the glucose produced by cellulose-decomposing species in excess of their own ability to absorb the products of decomposition. Some genera such as *Chaetocladium*, *Piptocephalis* and *Syncephalis* are parasitic on other members of the Mucorales. *Syncephalastrum* is typically saprophytic, but may also act as a parasite on other fungi. *Syzygites megalocarpus* Ehrenb. (= *Sporodinia grandis*) can frequently be found on decaying toadstools.

While members of the Mucorales are widely distributed on a worldwide basis, *Choanephora* and *Cunninghamella* are found in the soil in tropical and sub-tropical areas.

3. Ascomycotina

(a) *Hemiascomycetes*. The yeasts constitute the majority of the Hemiascomycetes which are concerned with the early stages of colonization of higher plants, forming a large proportion of the fungal population on leaves and fruits. Reviews have recently been published on their taxonomy by Kreger-van Rij (1969), their distribution in terrestrial and aquatic environments by Carmo-Sousa (1969), and their presence on living plants by Last and Price (1969).

(b) *Plectomycetes*. The parasitic Erysiphales grow almost exclusively on the surfaces of their hosts, obtaining their nutrients from haustoria which are formed in the epidermal cells. It would be interesting to know if the numerous minute punctures, produced by the infection pegs, have any stimulating effect on the eventual rate of decomposition of the host leaves.

Equally the mat of mycelium formed on the plant surface may keep potential saprophytes off the leaves and so retard decomposition.

Aspergillus and *Penicillium* are normally included in the Deuteromycetes. Those species which produce perfect states, however, are good examples of the Eurotiales, and they therefore will be considered here. Apart from the industrial and medical usage of their fermentation products, species of these genera are important economically for their deterioration of food, textiles and other substrates important to man. They are also widespread and abundant in the soil, with *Aspergillus* more common in warmer soils and *Penicillium* more frequent in temperate and wetter soils. Both genera owe their ubiquity to several features which they possess in common: an ability to grow on substrates with a relatively low moisture content (e.g. 82% r.g. for *P. expansum* Link), over a wide range of temperature (−3°C–35°C for *P. expansum*) and pH (e.g. *in vitro* from 2·0–10·0 in *P. cyclopium* Westling) and on a range of substrates; a high level of sporulation; rapid germination of conidia; antibiotic metabolites. Amongst these metabolites, penicillin is important medicinally, but aflatoxin, produced by *Aspergillus flavus*, for example on groundnuts, may be carcinogenic.

One of the common species of *Penicillium*, *P. cyclopium* Westling, may be taken as an example of a widespread species with a remarkable range of attributes. Domsch and Gams (1972) have recorded its worldwide occurrence in acid leaf litter and calcareous habitats, in saline estuaries and polluted streams, as well as in sand-dunes and arable soils. On higher plants, it has been found on roots, on wood pulp, hay and straw, and is frequent on stored wheat grain. It has been described as osmophilic and can grow at 81–84% r.h., and it has been shown to utilize pectin, starch, xylan, carboxymethyl cellulose, and filter paper, although its role as a cellulose decomposer is uncertain. An important attribute in decomposition of plant litter is its ability to grow on 5% tannin as the sole C source. It produces many metabolities which have antibiotic characteristics, and it is antagonistic to numerous fungi and bacteria *in vitro*.

There are many other common species of *Aspergillus* and *Penicillium* with a comparable range of attributes which would account for their ubiquity.

Other members of the Eurotiales include *Ceratocystis ulmi* (Buism.) C. Moreau, the causal agent of Dutch Elm Disease, and in the family Gymnoascaceae, *Byssochlamys fulva* Olliver & G. Smith, a soil-borne fungus which can cause spoilage in canned fruit: it is able to survive high temperatures and can grow at low oxygen tensions.

(c) *Pyrenomycetes*. Some members of the Pyrenomycetes are parasitic on plants (e.g. *Claviceps purpurea*, *Epichloe typhina* (Fr.) Fr.) or on animals (e.g. *Cordyceps militaris* (L.) Link on caterpillars). Others are widespread saprophytes, which are often or normally recorded on dung (e.g. *Sordaria*

fimicola (Rob.) Ces. & de Not.), *Podospora minuta* (Fr.) Niessl., *Poronia punctata* (L.) Fr.) while members of the genus *Chaetomium* are regularly isolated from soil, seeds and from almost any substrate which contains cellulose. Consequently it is a fungus of great economic importance, for example on textiles and military equipment. *Hypocrea pulvinata* Fuckel grows on the dead sporophores of *Piptoporus betulinus* (Bull.) Karst., a member of the *Polyporaceae* which grows on birch trees (*Betula* spp.).

The great majority of the other members of the Pyrenomycetes occur on wood (see Kaarik, Chapter 5). Many of them are primary colonists and amongst these are some parasites, such as *Nectria galligena* Bres. on apple and pear, *Daldinia concentrica* (Bolt.) Ces. & de Not. mainly on ash, and *Ustulina deusta* (Fr.) Petrak on beech.

Amongst the Pyrenomycetes which occur on wood, some are confined to one type of tree. Thus *Xylosphaera carpophila* (Pers.) Dum. is confined to fallen beech mast, *Cryptosphaeria eunomia* (Fr.) Fuckel is found on *Fraxinus*, *Diatrypella quercina* (Pers. ex Fr.) Cooke on *Quercus*, *Eutypa acharii* Tulasne on *Acer*, *Hypoxylon fragiforme* (Pers. ex Fr.) Kickx on *Fagus* and *Quaternaria quaternata* (Pers. ex Fr.) Schr. on *Fagus*.

Other species occur predominantly on one host, but are recorded on others, including *Diatrype disciformis* (Hoffm. ex Fr.) Fr. which is typically found on *Fagus*, but has been collected on *Quercus*, *Acer* and locally *Betula*, and *Hypoxylon fuscum* (Pers. ex Fr.) Fr. is normally collected on *Corylus*, but also occurs on *Alnus*. Yet other species are plurivorous, occurring on many types of wood. These include *Diatrype stigma* (Hoffm. ex Fr.) Fr., *Hypoxylon rubiginosum* (Pers. ex Fr.) Fr., *H. semi-immersum* Nitschke and *Xylosphaera hypoxylon* (Linn.) Dum.

These fungi are predominantly colonists of newly dead tissues and are "fungi of first incidence". Their stromata containing the perithecia are immersed in or erumpent from the bark. Some, however occur on both bark and decorticated wood (e.g. *Diatrype stigma*, *Hypoxylon multiforme* (Fr.) Fr.) while others only occur on the bare wood (e.g. *H. semi-immersum*).

A comprehensive account of the taxonomy and habitats of these fungi and of the Discomycetes has been given by Dennis (1960).

4. Basidiomycotina

The most commonly seen members of the Basidiomycotina on and associated with plant remains are members of the Agaricales (toadstools) and Aphyllophorales or Polyporales (bracket fungi). Both have the hymenium of basidia, upon which the spores are produced, freely exposed at maturity and they are consequently grouped together in the Hymenomycetes. In the Gasteromycetes, the hymenium is enclosed within the

sporophore. Here are included the Lycoperdales (puff-balls), Scleroderma-tales (earth balls), Phallales (stink horns) and Nidulariales (bird's nest fungi).

Some of the toadstools form symbiotic, mycorrhizal associations with the roots of higher plants, especially with trees (see Harley, 1969). Many of the bracket fungi are pathogens on trees (e.g. *Fomes annosus*, *Piptoporus betulinus* and *Polyporus squamosus* Fr.), as are some toadstools (e.g. *Armillaria mellea*) and cause considerable economic damage in the timber industry. *Serpula lacrimans* has been described as one of the most serious causes of timber deterioration in buildings, as it is the causal agent of dry rot (see Cartwright and Findlay, 1958).

Although toadstools and other Basidiomycetes are plentiful in fields and woods, and their mycelia can be seen in great quantities in leaf litter, these fungi are rarely recorded during normal isolation procedures. However, Warcup (1959) has isolated mycelia from soils and roots, using Warcup's (1957) hyphal isolation method and also a sieving and a flotation method to obtain sclerotia, and from direct plating of rhizomorphs. Warcup and Talbot (1962) identified 20 Basidiomycetes representing 18 genera which were isolated by these methods.

The fungi were mostly members of the Hymenomycetes, from all three orders recognized by Webster (1970), and two—*Cyathus stercoreus* (Schur.) de Toni and *Sphaerobolus stellatus* Tode ex Pers.—were members of the Nidulariales in the Gasteromycetes.

The occurrence of toadstools in woods has been recorded by Hora (1959), and in an apple orchard by Bond (1972). They undoubtedly play a large part in the breakdown of litter in these localities. *Coprinus cinereus* (Sch.) Gray and other species of *Coprinus* and of *Panaeolus* regularly occur on dung (see Lodha, Chapter 7).

Members of the Aphyllophorales are generally to be found on wood where they are the causal agents of brown rots (e.g. *Trametes serialis* Fr.) where the cellulose and associated polysaccharides have been destroyed, leaving the lignin, and white rots where the lignin has been degraded. The lignin-decomposers also attack the cellulose slowly and Cartwright and Findlay (1958) said that *Polystictus hirsutus* Fr. was able to attack cellulose more quickly than *Trametes pini* (Thore) Fr.

5. Deuteromycotina

The generally accepted grouping of the Deuteromycotina (Fungi Imperfecti) separates those species in which there is a protective covering around the conidiophores (Coelomycetes) from the Hyphomycetes, in which the conidiophores may or may not be grouped together, but in which there is no surrounding wall.

Members of the Coelomycetes which possess pycnidia are placed in the Sphaeropsidales, and these are frequently found on newly dead plant tissues. They can also be isolated from the soil. Grove (1935, 1937) gave a comprehensive account of the occurrence of these fungi on plants and Morgan-Jones *et al.* (1972) gave recent descriptions of selected genera.

Within the Hyphomycetes, the artificial system of Saccardo (1886) has long been used for purposes of identification and classification. There have been various attempts made to find a more natural system of classification (see Mason, 1937; Hughes, 1953; Tubaki, 1958). Arising from these, Barron (1968) published a comprehensive account of soil-borne Hyphomycetes arranged in groups which are distinguished from each other by the ontogeny of the conidia, regardless of their pigmentation. Saccardo's system, with emphasis on conidium pigmentation, had some ecological significance, as fungi with dark hyphae and/or conidia tend to predominate in soils subjected to high levels of insulation (Nicot, 1960) and on plant parts above the ground (Pugh and Williams, 1968; see also Ellis, 1971).

Members of the Deuteromycotina are very common and widespread. In his "Manual of Fungi", Gilman (1957) indicated that in the soil they comprised almost 57% of the species recorded, mainly drawing his results from the use of non-selective media and the soil dilution technique. With the introduction of a selective medium their occurrence rose to over 80% of the total number of isolations (see Pugh, 1969).

The observed life cycle of the Fungi Imperfecti is one in which conidia are produced on a mycelium, are dispersed and germinate to produce a new mycelium. The stage of sexual reproduction either does not occur, as in the self-incompatible strains which arise from single ascospores of *Neurospora crassa* Shear & Dodge, for example, or the sexual and asexual reproductive phases of the life cycle have not yet been associated. There is scope for further studies in this field, but it will not be straightforward, as several imperfect spore-forms may be associated with one generic perfect state, and conversely, one imperfect state may occur in several perfect genera (see Pugh, 1969). Webster (1970) omitted consideration of the Deuteromycotina from his account of the fungi, preferring to deal with imperfect states as part of the life-cycle of the perfect states which he discussed. There is a long way to go before this aim can be fulfilled even reasonably completely, and then, as Mason (1937) put it, "If we could consistently predict the Perfect genus by an inspection of its conidia, there would be no need for an Imperfect classification at all."

B. Biological Classification

The behaviour of fungi can be used to place them into categories which are essentially nutritional, such as parasites and saprophytes, or into

primary or secondary colonizers of substrates. There are also broad ecological groups which result from the interaction of the behaviour of the fungi and the environments in which they can grow.

In studies of fungi in the soil the concept arose of substrate relationships, with fungi colonizing the most readily available foods first, and being succeeded in waves by other species able to decompose in turn the more recalcitrant substrates. Thus the simple soluble carbohydrates would be used by the "sugar fungi", which would be followed by those able to attack cellulose, lignin and humus. The "sugar fungi", with their ability to "flare-up" rapidly on newly added substrates fall into the category of zymogenous organisms as described in Winogradsky's ecological grouping of soil bacteria. Those fungi able to utilize the more stable substrates such as cellulose and lignin, would grow more slowly and steadily over a longer period of time, and would form the bulk of his autochthonous flora. While such a general succession can be seen during the colonization of dung, Harper and Webster (1964) showed that the fungal sequence was a reflexion of the minimum time from the commencement of growth of the fungi until the appearance of the sporing structures. The succession on leaves and litter frequently omits the "sugar-fungi". Indeed the primary colonizers can produce a wide range of enzymes, including cellulase, cutinase, pectinase and protease, as well as enzymes for sugars and other carbohydrates (see Pugh *et al.*, 1972). Griffin (1972) has also criticized the division of soil fungi into zymogenous and autochthonous categories; as he said, "all soil fungi for which we have much information are zymogenous and one could be forgiven for doubting if truly autochthonous forms exist".

Another form of biological classification was used by Reinking and Manns (1933) to separate "soil-inhabiting" and "soil-invading" species of *Fusarium*. Garrett (1956) recognized that the "soil invaders" were really root-inhabiting species, and put forward a scheme in which he showed the ecological relationships between root-inhabiting, root-disease and soil-inhabiting fungi.

Physiological criteria can also be used to distinguish broad ecological groups of fungi. Thus while most fungi are mesophilic in their temperature requirements, the thermophiles grow at high temperatures and the psychrophiles grow in cold conditions.

V. Physiology

A. Introduction

The decomposition of a substrate by a fungus requires the presence of both, in an environment which is suitable for the fungus to grow, produce the necessary enzymes and absorb soluble nutrients. In considering the

role of fungi on plant litter the nutrients in that litter will normally be sufficient for growth, even if the balance of elements may not be optimal at any given moment, while in the soil there may well be a starvation diet away from the influence of living roots. The limiting factors will vary with the geographical and topical locality of the substrate. On a leaf surface, desiccation and harmful radiations may be most important; in the soil, the water regime, the prevailing temperature, oxygen supply, hydrogen ion concentration and the presence of fungistatic or fungitoxic substances will all help determine whether the fungus can grow. Its saprophytic survival will depend on its competitive ability as well as on endogenous characters such as the ability to produce enzymes in what is almost certainly a far from ideal environment. Indeed, it has been said that fungal ecology is the study of fungal physiology under the worst possible conditions.

B. Carbon : Nitrogen Ratio

Carbon is plentiful in plant remains, particularly in cellulose, which may form 15–60% of the dry weight, hemicelluloses (10–30%) and lignin (5–30%), as well as being present in soluble carbohydrates. Nitrogen represents a much smaller part of the plant remains, being present mainly in proteins and amino acids. Succulent, herbaceous plants will have relatively more nitrogen; woody plants and particularly trees will have relatively less. Older plants generally will have relatively more carbon and less nitrogen than younger plants. In the decomposition of litter, the availability of nitrogen will determine the speed of the mineralization processes. Litter with a good supply of nitrogen (i.e. C:N ratio of 30:1 as in leguminous plants) will decompose quickly, but when the supply is poor (i.e. a C:N ratio of >200:1 in wood) the rate will be slow and nitrogen may be taken up from the surrounding soil. In the composting of plant material additional nitrogen is necessary for rapid decomposition. As mineralization proceeds, the C:N ratio eventually falls to a level of about 10:1 because carbon is given off as CO_2 while the nitrogen which has been utilized by the fungi is bound up in the mycelium and will be used by succeeding organisms after the death of the hyphae. This subject has been discussed amongst others by Burges (1958) and Alexander (1961).

The type of growth of the fungi is determined by the nature of the substrate, so that they tend to grow rapidly, vegetatively, on a new substrate, and to sporulate as the nutrient status of the substrate is reduced. Often a high level of nitrogen suppresses the production of spores. It has also been shown to curtail the survival time of six root rot fungi in straws buried in the soil (Garrett, 1972). A study of fungal preferences for different C:N ratios was carried out by Kaufman and Williams (1963), who found that

more fungi were isolated from soils with a narrow C:N ratio, where species of *Botryotrichum*, *Chaetomium*, *Masoniella*, *Stysanus* and members of the *Penicillium rugulosum* series were more prevalent. In soils with a wide C:N ratio they more frequently found species of *Actinomucor*, *Coniothyrium*, *Phoma*, *Trichoderma* and the *Penicillium funiculosum* Thom series. *Circinella* sp., *Humicola* sp. and *P. lilacinum* Wehmer series were favoured by specific C:N ratios.

The source of nitrogen can also be important. Most fungi can utilize ammonium salts or nitrates (although some of the water moulds do not use nitrate nitrogen). Ammonium salts are generally more readily used, and the addition of ammonia to a growth medium in which *Scopulariopsis brevicaulis* (Sacc.) Bain. was being grown with nitrate suppressed the nitrate assimilation. The whole question of the utilization of nitrogen sources by fungi has been fully discussed by Nicholas (1965).

C. Fungal Metabolites

During their growth fungi produce many metabolities which may be useful to man (e.g. penicillin) or harmful (e.g. aflatoxin). They have been shown to produce auxins (I.A.A. and I.A.N.) when grown *in vitro* in the presence of tryptophan (see Buckley and Pugh, 1971). Auxin production *in vivo* could have widespread effects in the ecosystem.

The range of substrates upon which fungi can grow is dependent on their enzyme systems. While virtually all fungi can utilize glucose, increasing complexity of the substrate requires the production of particular enzymes, the demonstration of which, in the laboratory at least, indicates the potential to use that substrate in the field. As cellulose forms such a large part of plant remains and particularly of man-made litter such as textiles and paper products, cellulases are very important in nature. The occurrence of cellulose-decomposing fungi has been studied by many workers. Earlier studies were collated by Siu (1951), while some methods for detecting cellulases are given in Kelman (1967). Other enzyme systems that are important in plant litter decomposition include cutinase and pectinase, which are found, for example, in plant pathogens and phylloplane fungi, amylase, lipase, proteinases and saccharase which degrade plant cell contents. The decomposition of lignin (a highly complex phenolic polymer) requires a phenol oxidase, and phenolases, produced by white-rot fungi are involved in the breakdown of lignin and other polyphenols (Hurst and Burges, 1967). Polyphenols and particularly tannins, are responsible for the unpalatability of many leaves to the soil fauna. They are broken down to catechols and gallic acid, for example by *Penicillium expansum* Link.

D. Radiation

1. Light

The general conditions for growth of fungi in the laboratory, on a bench, or in an incubator, normally do not make allowance for the effects of light. In certain circumstances, however, light can play an important part in the life cycle of fungi. Most coprophilous fungi, for example, have a mechanism which ensures that their spores are discharged towards a light source. In *Ascophanus* the asci are orientated towards light; in *Pilobolus* the sporangiophore grows so that the sporangium is discharged towards a light source; in *Sordaria* the neck of the perithecium grows so that the ascospores are similarly discharged. The germination of spores is increased by light in most cases, although the germ tube of *Botrytis cinerea* is negatively phototropic. Light at high intensities generally retards mycelial growth, although there are isolated reports of stimulation. Some hyphae are positively phototropic, and may show zonation if they are grown in an alternating light and dark regime (e.g. *Alternaria brassicae* (Berk.) Sacc.). In other fungi, such as *Fusarium* and *Trichoderma*, sporulation is dependent upon an exposure to light. Page (1965) has briefly reviewed the main effects of light on fungal growth.

2. Ultraviolet Radiations

Ultraviolet radiations present in daylight are generally harmful and can be lethal to fungi at a wavelength of around 2600 Å. The mechanism of this action and its genetic effects have been discussed (Pomper, 1965). In fungal ecology the lethal action can be avoided if the fungus is pigmented, or if it produces its spores in a protective covering. Nicot (1960) drew attention to the prevalence of strongly pigmented members of the phragmo- and dictyospored Dematiaceae, members of the Sphaeropsidales, and dark sterile hyphae in desert sands in North Africa. In a study of fungi on *Salsola kali* L. growing in coastal sands in Britain, Pugh and Williams (1968) showed that dematiaceous fungi (*Alternaria*, *Botrytis*, *Cladosporium*, *Epicoccum*, *Stemphylium*) predominated on the aerial parts of the plant, while *Cephalosporium* and *Fusarium* were more common on the roots. They postulated that the pigmented fungi on the aerial parts were protected against, or derived benefit from, the ultraviolet radiations to which they were exposed. Similarly on leaf surfaces, Pugh and Buckley (1971*b*) have indicated that the phylloplane fungi *Alternaria*, *Botrytis*, *Cladosporium* and *Epicoccum* are protected by their pigmentation, *Sporobolomyces* may derive benefit from the presence of carotenoids and from its growth pattern, with outer cells protecting inner cells in a clump, while *Aureobasidium* on an exposed surface forms pigmented microsclerotia which are resistant to u.v.,

and can also be isolated from within the veins, where it will be protected by the cells of the leaf. Hyaline spores are more susceptible to u.v. damage than are pigmented spores, where the melanin in the wall acts as a screen. In multicellular spores, such as those of *Alternaria*, *Epicoccum* and *Stemphylium*, some cells are always shielded by others.

E. Temperature

The temperature relationships of fungi have been discussed by Togashi (1949). The great majority of fungi are mesophilic in their temperature requirements, with a minimum temperature for growth generally between 5°C and 10°C, a maximum between 30°C and 40°C, and an optimum between 25°C and 35°C. Outside these temperature ranges, some fungi, the psychrophiles, can grow at low temperatures. These have been found on frozen foods at temperatures as low as −6°C (*Cladosporium herbarum*), while *Alternaria tenuis* auct. and *Botrytis cinerea* have been recorded at −2°C. Pugh *et al.* (1972) have drawn attention to the ability of the common phylloplane fungi to grow at low temperatures, and Deverall (1968) has discussed the growth of fungi in cold environments.

At the other extreme, the thermophiles have been defined by Cooney and Emerson (1964) as having a maximum growth temperature at or above 50°C and minima above 20°C. They regarded as thermotolerant those species which had a maximum temperature near 50°C but a minimum below 20°C. This group more or less coincides with the psychrotolerant thermophiles of Apinis (1963) and includes such common fungi as *Aspergillus fumigatus* Fresen. The thermophiles occur in a number of agricultural and industrial processes, being found for example on stored grain, fermenting cocoa, and in accumulations of organic material such as composts (see Chang and Hudson, 1967).

F. Water Relationship

The influence of water on fungi in the soil has been thoroughly discussed by Griffin (1972). In dry litter on the soil surface, or still attached to the plant in an aerial environment, however, the moisture levels may fluctuate greatly and at their lower levels may be limiting to fungal germination and growth. A similar limiting condition is aimed at in substrates useful to man (paper products, textiles, timber and stored food grains, for example). In these situations a small variation in moisture level can be sufficient to allow germination to occur. In the case of dry rot in building timbers the moisture level around floor joists can be increased by insufficient ventilation, or by a circumvention of the damp course (by a flower border being

banked up above its level, for example). Once the water content of the wood reaches fibre saturation point (about 27% of the dry weight of the wood) germination of spores of *Serpula lacrimans* can occur. The fungus can then grow onto and into dry wood, obtaining its water by breaking down the cellulose, and producing excess water which forms drops on the mycelium. This makes eradication of this fungus much more difficult than the wet rot fungi such as *Coniophora cerebella* Pers. which rely on an external supply of water, and can therefore be controlled by rectifying conditions so that the wood can dry out.

Species of *Penicillium* and particularly of *Aspergillus* are extreme xerophiles, able to grow at lower moisture levels than other fungi. There is a direct relationship between the osmotic potential of the hyphae and their ability to grow at a low relative humidity. Thus the suction pressure of hyphae of species of these two genera has been calculated at 217 atm (see Hawker, 1950) and *Aspergillus* has been shown to grow on media with an osmotic pressure of 100 atm. Osmophilic fungi, particularly yeasts, are other examples of organisms adapted to low moisture regimes, where there is a state of physiological drought. In terms of the deterioration of fabrics, paper and cereal grains in storage, a rise in the level of the relative humidity to about 80% can be sufficient to allow fungal germination. In goods packed in non-porous material a fall in temperature can raise the humidity above the danger level.

There have been various studies on the effects of moisture levels on spore germination, hyphal growth and sporulation, particularly in plant-pathogenic fungi.

Similar detailed studies are needed for many of the fungi which are involved in the saprophytic breakdown of plant litter. These could, with advantage, be extended into autecological studies of individual species. In this respect the compilation of available knowledge about more than 200 species of soil fungi by Domsch and Gams (1972) provides an easily accessible source of information and points the way for future development.

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